Changes in biological parameters of Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the Gulf of Mexico: evidence for density-dependent growth and maturity?

John K. Carlson[A,B] *and Ivy E. Baremore*[A]

[A]NOAA/National Marine Fisheries Service, South-east Fisheries Science Center, 3500 Delwood Beach Road, Panama City, FL 32408, USA.
[B]Corresponding author. Email:john.carlson@noaa.gov

Abstract.   Biological parameters of the Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the northern Gulf of Mexico were re-examined to test for potential changes due to density dependent responses. Biological data from published studies in the Gulf of Mexico collected during the period 1979–1984 were compared with data collected during the period 1998–2001. For combined sexes, the von Bertalanffy growth parameters were $L_\infty = 110.8$ cm total length, $K = 0.39$ year^{-1} and $t_o = -0.86$ year during 1984 and $L_\infty = 94.0$ cm total length, $K = 0.73$ year^{-1} and $t_o = -0.88$ year during 1998–2001. Median size for males and females at maturity decreased from approximately 78.3 and 80.2 cm total length (TL), respectively, in 1979–1980 to 72.6 and 75.8 cm TL, respectively, in 1998–2001. Age at maturity for combined sexes also decreased from 2.3 years in 1979–1980 to 1.4 years in 1998–2001. Litter size was similar between periods (5.0 embryos), as was the average size of embryos close to parturition (32 cm TL; 130–150 g). Growth rates using observed mean size-at-age data were higher from 1998–2001 for early ages (0–2.5 years). The observed decrease in maturity and increased growth rate lends support to the hypothesis of a compensatory response, although it could not be fully determined whether the response was due to differences in methodology among studies, anthropogenic influences or natural causes.

Extra keywords: age, compensatory, exploitation, small coastal shark.

Introduction

Small coastal sharks in waters of the US Atlantic Ocean and Gulf of Mexico were determined in 1993 to be fully utilized (National Marine Fisheries Service (NMFS) 1993). Subsequent reductions in commercial quotas for blacktip shark *Carcharhinus limbatus* and sandbar shark *Carcharhinus plumbeus* have caused increased exploitation of the Atlantic sharpnose shark *Rhizoprionodon terraenovae*, the most abundant small coastal shark. For example, commercial harvests increased from 42.5 metric tonnes in 1995 to 110.8 metric tonnes in 1999 (Cortés 2002a). Recreational catches of Atlantic sharpnose shark have also intensified from an estimated 43 000 sharks in 1981 to 1 224 000 sharks in 2000 (Cortés 2002a). Atlantic sharpnose sharks suffer considerable mortality as bycatch in various fisheries (Cortés 2002a) and this mortality likely exceeds the recorded landings for this species. Moreover, a recent stock assessment of Atlantic sharpnose sharks found their abundance to be between 0.6% and 0.8% of virgin biomass (Cortés 2002a). Similarly, Simpfendorfer and

Burgess (2002) reported that, in 2000, the population was likely to be approximately 69% of that in 1972. Because the abundance of Atlantic sharpnose shark has declined, perhaps due to increased mortality, it would be reasonable to expect changes in biological parameters due to a density dependent compensatory mechanism.

There are several mechanisms by which density dependent regulation in shark populations may occur. Holden (1973) hypothesized that if dogfish populations are reduced, then compensatory increases in fecundity and growth rate (which, in turn, induce earlier maturity) or decreases in natural mortality may take place as a result of decreased predation, reduced competition or increases in available food. Holden (1973) proposed that a change in fecundity was the density dependent mechanism for controlling populations of the spiny dogfish *Squalus acanthis* off Norway. However, Wood *et al.* (1979) used a series of theoretical simulations to suggest that natural mortality was the mechanism for regulating spiny dogfish populations off British Columbia, Canada. Walker (1992)

predicted sustainable fishing on populations of gummy shark *Mustelus antarcticus* when allowing for density dependence to act on survival of pre-recruit age classes.

Although density dependent regulation has been documented for a variety of species of teleosts (for a review, see Rose *et al.* 2001), empirical evidence of density dependent compensation in sharks is very rare. A study on the age and growth of the sandbar shark *Carcharhinus plumbeus* found an increase in juvenile growth rate after exploitation, but this was not accompanied by a decrease in age at maturity (Sminkey and Musick 1995). Although these results are conflicting (perhaps due to methodology; Cortés 2002*b*), the possibility exists that changes due to density dependence are much more difficult to quantify for longer-lived elasmobranchs, like the sandbar shark, which does not reach age at maturity until 13–15 years and has a generation time of 21 years (Cortés 1998). Thus, density dependent compensation in sharks, if it occurs, may be easier to detect for a relatively short-lived elasmobranch, like the Atlantic sharpnose shark, which has a generation time of 5.8 years (Cortés 1995). The objectives of the present paper are to update age, growth and reproductive parameters of the Atlantic sharpnose shark in the northern Gulf of Mexico and to test for potential compensatory changes in biological parameters using empirical data.

Materials and methods

Atlantic sharpnose sharks occur year round in the Gulf of Mexico and current tagging evidence suggests sharks do not make long distance movements and generally occur over the same region (Kohler *et al.* 1998; J. K. Carlson, unpublished data). Previous studies (Parsons 1983, 1985; Branstetter 1987) sampled Atlantic sharpnose sharks from the northern Gulf of Mexico in areas around Galveston Bay, TX (approximately 29°10′N 94°50′W) and Mobile Bay, AL (approximately 30°00′N 88°15′W). To avoid any bias associated with sampling in different regions, sharks were collected from the northern Gulf of Mexico (Galveston, TX to Panama City, FL; Fig. 1) during 1998–2001 using gill-nets (multiple panels of 8.9–20.3 cm stretched mesh sizes) and bottom longlines (100 no. 15/0 circle hooks). Captured sharks were placed on ice and returned to the laboratory for analysis. Sharks were measured to the nearest cm in several ways to determine body length (PC = pre-caudal length; FL = fork length; TL = total length; STL = stretched total length). Vertebrae were collected from the column between origin and termination of the first dorsal fin and reproductive condition was assessed following Parsons (1983). Males were considered mature if they possessed hardened, fully developed claspers. Females were regarded mature if they were gravid, had oocytes larger than 2.0 cm in diameter and the ovary was fully developed.

Preparation of vertebrae for enhancement and reading of growth bands was performed following Carlson *et al.* (2003). Growth bands were found to be most visible using a crystal violet stain on 0.5 mm sagittal sections. Based on a previous validation study (Branstetter 1987), we assigned ages assuming that: (*1*) the birth mark is associated with a pronounced change in angle in the intermedialia and is formed on an arbitrary birth date of 1 June; (*2*) growth bands (one narrow dark and one broad light mark) are formed once a year; and (*3*) narrow dark marks are deposited in winter. Ages were calculated using the algorithm age = birth mark + number of winter marks −1.5. If only the birth mark was present, age was assumed to be 0+. Both authors aged each
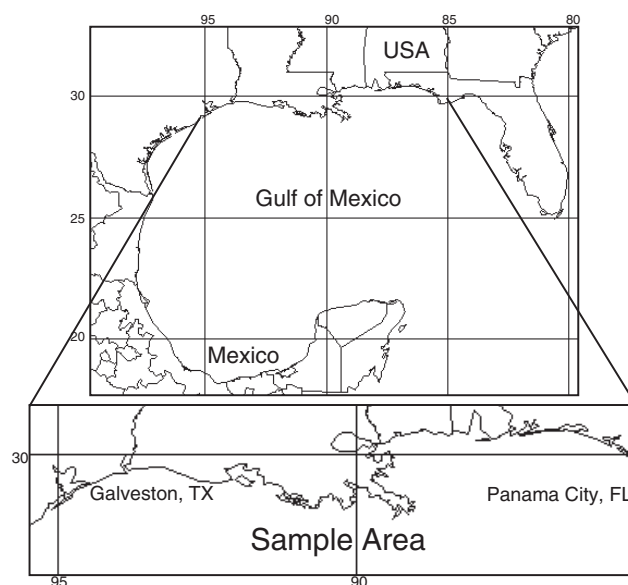

Fig. 1. Sampling area for Atlantic sharpnose sharks in the northern Gulf of Mexico.

specimen independently without knowledge of its length or sex. Two sets of age readings were made, the second set after consultation between the authors. The index of average percent error (Beamish and Fournier 1981) and the percentage of disagreements by ±*i* rings between authors were computed for the first set of age readings.

Growth for male and female sharks was expressed using the von Bertalanffy growth model (von Bertalanffy 1938) fitted to observed size-at-age data using the equation:

$$L_t = L_\infty(1 - e^{-K(t-to)})$$

where L_t is the predicted length at time *t*, L_∞ is the theoretical asymptotic length, *K* is the growth coefficient and t_o is the theoretical age at zero length. Growth model parameters were estimated using Marquardt least-squares non-linear regression. Comparison of growth curves between sexes was performed using χ^2-tests of log-likelihood ratios (Kimura 1980). Theoretical longevity was estimated as the age at which 95% of L_∞ is reached ($5(\ln2)/K$; Fabens 1965).

Median TL at maturity for male and female sharks was determined by fitting the following logistic model to the binomial maturity data (immature = 0; mature = 1):

$$Y = 1/(1 + e^{-(a+bX)})$$

where *Y* is maturity and *X* is the TL (in cm; Mollet *et al.* 2000). Median TL at maturity was expressed as −*a*/*b*. The model was fitted using least-squares non-linear regression. Length was back-transformed to age using data from the present study (1998–2001) and from 1984 (Branstetter 1987) and the logistic model was fit to the corresponding age to determine median age at maturity. Reproductive effort was determined by examining litter size and quantifying the average size and weight of near-term embryos.

Comparison of biological parameters

Length-at-age data (*n* = 20) collected in 1984 by Branstetter (1987) and reproductive information (*n* = 149) obtained during 1979–1980 by Parsons (1983) were compared with data obtained in 1998–2001 (age and growth *n* = 304; reproduction *n* = 357) to test for differences in life

Table 1.   Parameters of the von Bertalanffy growth models for Atlantic sharpnose shark

Estimates are provided for models developed using observed size-at-age data obtained for male and female sharks from 1998 to 2001 and for combined sexes from 1998 to 2001 and 1984, with the 95% confidence interval given in parentheses. L is the theoretical asymptotic length, K is the growth coefficient and t_o is the theoretical age at zero length

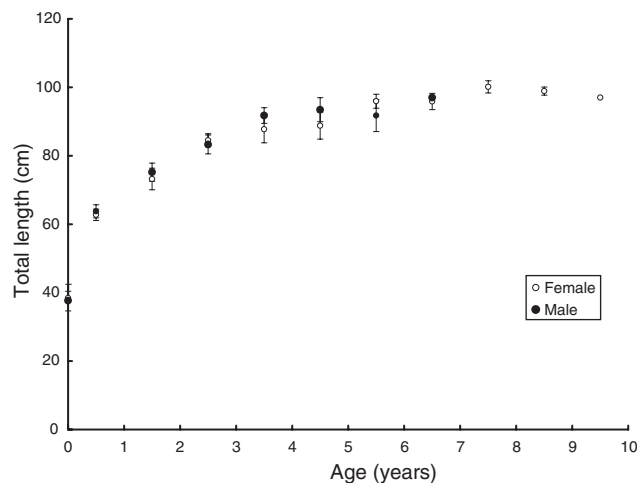|	L (cm)	K (years^{-1})	t_o (years)	n
1998–2001				
Female	95.62 (92.85, 98.38)	0.63 (0.51, 0.75)	−1.03 (−1.27, −0.79)	143
Male	91.95 (88.94, 94.96)	0.85 (0.66, 1.04)	−0.73 (−0.92, −0.54)	161
1984				
Combined sexes	110.80 (98.95, 122.70)	0.39 (0.24, 0.53)	−0.86 (−1.22, −0.49)	20
1998–2001				
Combined sexes	94.02 (91.93, 96.11)	0.73 (0.63, 0.83)	−0.88 (−1.03, −0.72)	304

Fig. 2. Von Bertalanffy growth functions for male and female Atlantic sharpnose sharks using observed size-at-age data from 1998 to 2001. Vertical bars are 95% confidence limits.

history traits. We used observed size-at-age data when comparing growth curves because of the uncertainties and complexities associated with using back-calculated lengths-at-age (e.g. Rosa Lee's Phenomenon; Walker *et al.* 1998). Growth curves for combined sexes were compared between sampling periods following Kimura (1980). Observed mean size-at-age and growth rates between ages were compared using Student's *t*-test (Zar 1984). Sex-specific median size and age at maturity (combined sexes) obtained through the logistic model were compared using *F*-tests (Mollet *et al.* 2000).

Results

Previous studies on the Atlantic sharpnose shark have reported information in TL (i.e. a straight line from the tip of the snout to the tip of the tail in a natural position); thus, our results are reported in natural TL to provide for direct comparison. We derived several morphometric relationships for comparison with other studies that used different lengths. Linear regression formulae were determined as FL = 1.081(PC)+0.784, TL = 1.158(FL) + 1.476 and STL = 1.007 (TL) + 2.167. All equations were highly significant ($P < 0.0001$) and had high coefficients of determination ($r^2 \geq 0.99$).

Biological parameters 1998–2001

The precision of band counts was high between authors. The first set of readings resulted in an average error of 3.1%. After consultation, agreement was reached in 304 out of 308 vertebrae (98.7%). Samples with disagreement were discarded.

Von Bertalanffy growth parameters for Atlantic sharpnose sharks were $L_\infty = 95.6$ cm TL, $K = 0.63$ year^{-1}, $t_o = -1.03$ year for females and $L_\infty = 91.9$ cm TL, $K = 0.85$ year^{-1} $t_o = -0.73$ year for males (Table 1). No significant differences in von Bertalanffy growth curves were found between sexes (log-likelihood ratio = 1.268; $P \geq 0.05$; Fig. 2). The maximum observed ages based on vertebral band counts were 9.5+ and 6.5+ years for females and males respectively. Theoretical longevity estimates were 5.5 years for females and 4.0 years for males using values obtained through von Bertalanffy growth models.

Median size at maturity was significantly larger ($P < 0.001$) for females (75.8 cm TL) than for males (72.6 cm TL; Table 2). The largest immature sharks were 86 and 80 cm TL for females and males, respectively, and the smallest mature sharks were 75 and 65 cm TL for females and males respectively. Fitting the logistic model to the corresponding age data resulted in a median age of maturity of 1.6 and 1.3 years for females and males respectively.

Comparison of biological parameters

Growth parameters for combined sexes derived for Atlantic sharpnose shark from 1998–2001 show that they attain a smaller theoretical maximum size (L_∞) and that they reach L_∞ at a faster rate (K) than conspecifics from 1984 (Fig. 3). Von Bertalanffy growth parameters were $L_\infty = 94.0$ cm TL, $K = 0.73$ year^{-1}, $t_o = -0.88$ year in 1998–2001 compared with $L_\infty = 110.8$ cm TL, $K = 0.39$ year^{-1}, $t_o = -0.86$ year. Significant differences in von Bertalanffy growth curves were found between time periods (log-likelihood ratio = 38.124; $P < 0.001$). Maximum age increased by 4 years (5.5 *v.* 9.5 years) from 1984 to 1998–2001.

Table 2. Summary of reproductive parameters for Atlantic sharpnose shark
Median total length and age at maturity was obtained using a logistic model fit to binomial maturity
data. Estimates are provided for data obtained for male and female sharks from 1998 to 2001 and
1979 to 1980 with 95% confidence intervals given in parentheses

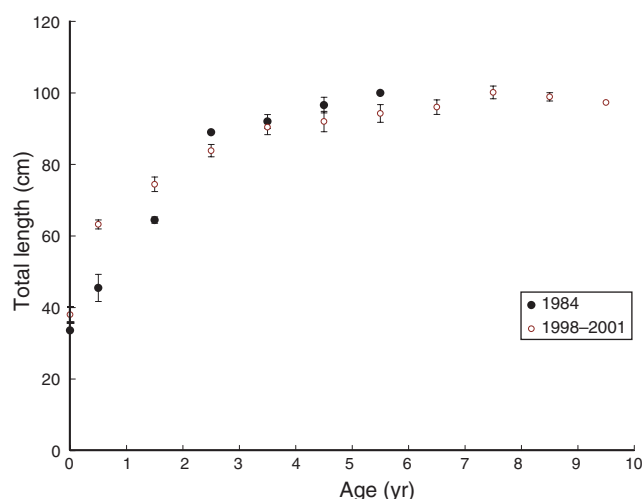|	Females	Males
1998–2001		
Median size at maturity (cm)	75.8 (67.5, 85.6)	72.6 (40.8, 130.7)
Median age at maturity (years)	1.6 (1.0, 2.7)	1.3 (0.7, 2.6)
n	171	186
1979–1980		
Median size at maturity (cm)	80.2 (78.2, 82.4)	78.3 (76.3, 80.3)
Median age at maturity (years)	2.3 (2.2, 2.6)	2.3 (2.1, 2.4)
n	88	59

Fig. 3. Von Bertalanffy growth functions for Atlantic sharpnose sharks (sexes combined) using observed size-at-age data from 1984 (Branstetter 1987) and 1998–2001 (present study). Vertical bars are 95% confidence limits.

Observed size-at-age was different between studies, but most ages were not significantly different ($P \geq 0.05$), in part due to small sample size in 1984 (Table 3). Among younger ages (<2.5 years), mean observed size-at-age was larger for 1998–2001. Beyond age 2.5, mean observed size-at-age was larger for the Atlantic sharpnose sharks from 1984.

Growth rates between early ages exhibited opposite trends between 1984 and 1998–2001. Average growth from observed mean size-at-age data was 25.2 cm TL from age 0 to age 0.5, 11.2 cm TL from age 0.5 to 1.5 and 9.4 cm from age 1.5 to 2.5 for those sharks obtained during 1998–2001. Sharks grew 11.9 cm TL from age 0 to age 0.5, 19 cm TL from age 0.5 to 1.5 and 24.5 cm from age 1.5 to 2.5 during 1984.

Estimates of size and age at maturity for male and female sharks from 1998 to 2001 were different from those in 1979–1980. Although sample size was larger for sharks collected during 1998–2001, samples were representative from all size classes (Fig. 4). Total length at which 50% of the population reached maturity decreased from approximately 80.2 cm TL in 1979–1980 to 75.8 cm TL in 1998–2001 for females (Fig. 5) and was found to be significantly different ($P < 0.01$). Median total length at maturity for males also decreased from 78.3 to 72.6 cm TL and was significantly different ($P < 0.01$). Using the combined age and growth models, median age at maturity decreased from 2.3 years in 1979–1980 to 1.4 years in 1998–2001 (Fig. 6; $P < 0.01$).

A significant exponential relationship was found between maternal TL and number of embryos (litter size = $0.047\exp^{(0.048)\mathrm{TL}}$; $r^2 = 0.65$; $P < 0.001$) for 1998–2001 (Fig. 7). Mean ($\pm$ s.d.) litter size was 5.0 ± 1.8 pups. The mean ($\pm$ s.d.) size of near-term embryos was 32.3 ± 2.1 STL and mean weight was 130.1 ± 29.8 g. Overall, litter size was similar between studies (5.0 embryos), as was the mean weight of near-term embryos (130.1 ± 29.8 g for 1998–2001 and 95–150 g for 1979–1980).

Discussion

Demographic studies have reported that elasmobranch population growth and productivity are most influenced by juvenile survivorship and age at maturity (Smith *et al.* 1998; Cortés 2002*b*). This type of compensation appears to be more relevant to sharks because sharks are limited by space available for increases in pup production (increased fecundity; Cortés 2002*b*). This trend seems to carry across to elasmobranchs that are oviparous. Frisk *et al.* (2002) showed that population growth rates for three species of skates from the north-west Atlantic Ocean were relatively insensitive to changes in fecundity. An increase in reproductive periodicity may be possible for some species, but Atlantic sharpnose sharks already possess an annual reproductive cycle. Although a comparison of survivorship was not possible, evidence from the present study suggests the mechanism for controlling density dependent regulation in Atlantic sharpnose shark is to increase juvenile growth, which, in turn, induces a decrease in size and age of maturity. Because

Table 3. Comparison of observed mean size at age for combined sexes from 1984 and 1998–2001
s.d., Standard deviation of the mean; l.c.l., lower 95% confidence limit; u.c.l., upper 95% confidence limit

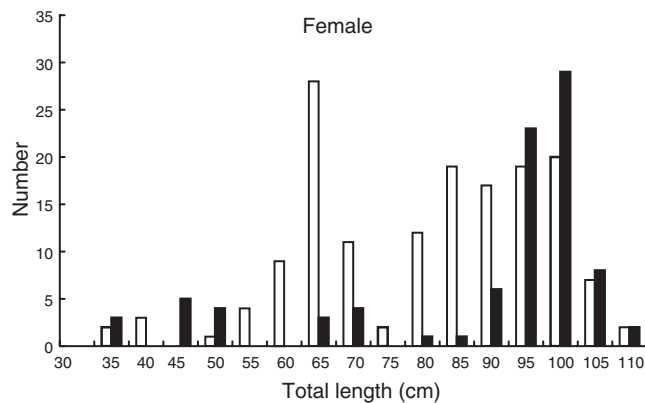|	Age										
	0	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5
1984	33.6	45.5	64.5	89.0	92.0	96.6	100.0				
s.d.	–	4.7	0.9	–	1.4	2.5	–				
l.c.l.	–	40.5	63.0	–	79.3	93.5	–				
u.c.l.	–	50.4	65.9	–	104.7	99.7	–				
n	1	6	4	1	2	5	1				
1998–2001	38.0	63.2	74.4	83.9	90.4	92.0	94.3	96.0	100.1	98.9	97.3
s.d.	5.7	6.1	7.7	6.4	6.2	5.8	3.9	3.8	1.8	0.8	–
l.c.l.	35.7	61.9	72.4	82.2	88.3	88.9	91.4	93.9	97.5	86.3	–
u.c.l.	40.4	64.5	76.6	85.7	92.6	95.2	97.2	98.3	102.9	111.7	–
n	26	90	55	53	33	16	10	14	4	2	1
P	–	≥0.05	<0.01	–	≥0.05	≥0.05	–				

Fig. 4. Length-frequency distributions for male and female Atlantic sharpnose sharks used for reproductive analysis from 1979 to 1980 (Parsons 1983: black bars) and 1998 to 2001 (present study: white bars).

Fig. 5. Total length at maturity of (*a*) male and (*b*) female Atlantic sharpnose sharks from 1979 to 1980 (Parsons 1983; solid line) and 1998 to 2001 (present study; dashed line), as expressed through the logistic model. The size at which 50% of the population is mature is indicated by an open circle for 1998–2001 and a solid circle for 1979–1980.

of their relatively small size, these sharks are likely more vulnerable to predation. Thus, the advantage of decreasing age and size at maturity is a greater chance that their offspring will survive to maturity and begin reproducing.

Reductions in the size of Atlantic sharpnose shark populations may result in decreasing intraspecific competition. Sequentially, lower competition may provide greater food intake per individual, enabling sharks to grow faster. Growth for earlier ages (0.0–0.5, 0.5–1.5 years) from 1998–2001 were up to twice as fast as those determined from 1984 based on observed size-at-age data. The faster growth observed could be due to a food effect mechanism. Juvenile sharks have been shown to increase their growth rate when given a higher quantity of food. For example, young-of-the-year blacktip reef sharks (*Carcharhinus melanopterus*) increased their growth from 0.33 to 0.57 mm day^{-1} when fed a greater quantity of food on a weekly basis (Taylor and Wisner 1988). In addition, young lemon sharks (*Negaprion brevirostris*) kept under controlled conditions
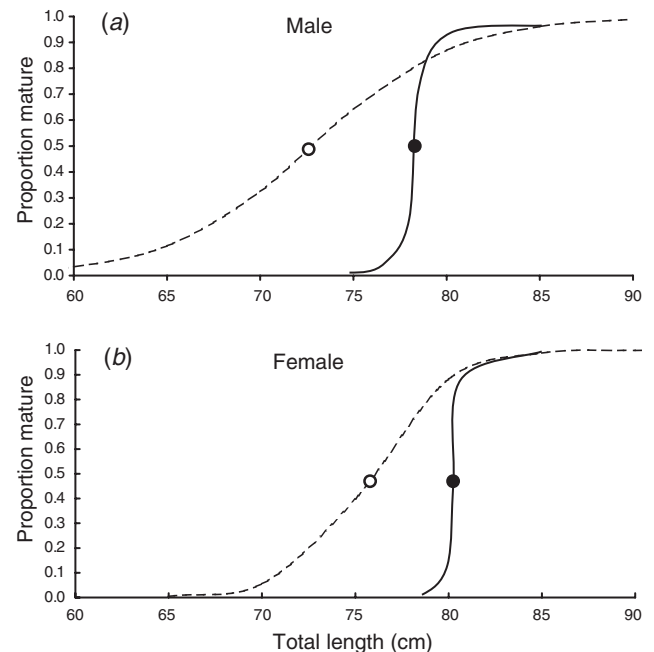
increased their daily growth rate when daily feeding rate was increased (Cortés and Gruber 1994).

Using life history data from Parsons (1983) and Branstetter (1987), Cortés (1995) showed that intrinsic rate of increase for the population of Atlantic sharpnose sharks was $r = 0.044$ year^{-1} with a generation time of 5.8 years, under a best-case scenario. Cortés (1995) further concluded that, at this intrinsic rate of increase, the population would not be able to withstand the level of fishing mortality for the late 1980s and early 1990s. By incorporating the increases in
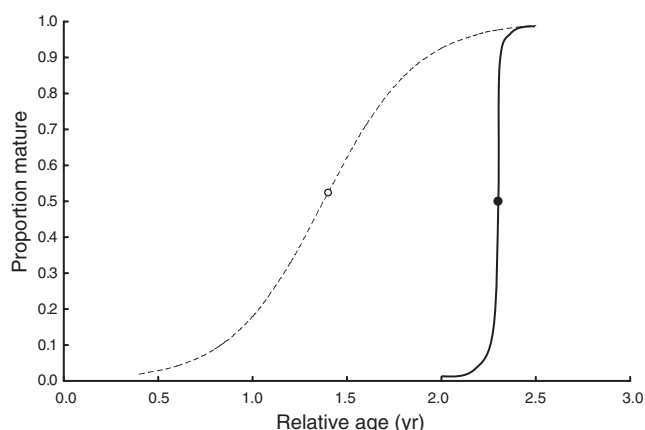
Fig. 6. Relative age at maturity for Atlantic sharpnose sharks (combined sexes) from 1979 to 1980 (Parsons 1983; solid line) and 1998–2001 (present study; dashed line) as expressed through the logistic model. The age at which 50% of the population is mature is indicated by an open circle for 1998–2001 and a solid circle for 1979–1980.
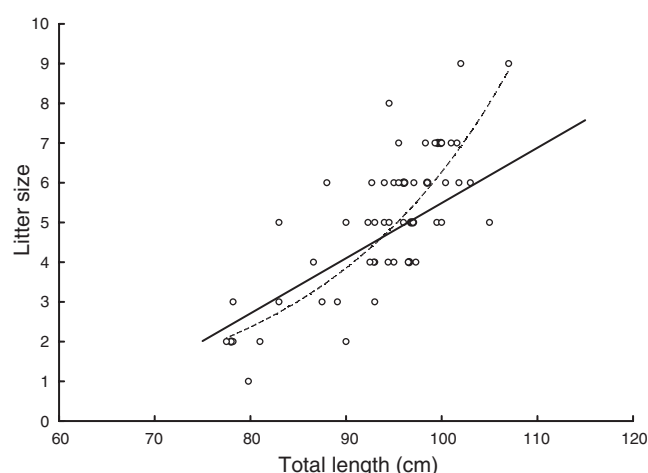

Fig. 7. Relationship between maternal length (TL) and litter size (number of embryos). Dashed line and circles indicate the data for 1998–2001; the solid line represents the relationship (litter size = $-8.4109 + 0.1396$ (TL)) derived by Parsons (1983).

growth and decreases in maturity from our study and following the methods of Cortes (1995), in the absence of fishing, preliminary estimates are $r = 0.120$ year^{-1} with a generation time of 3.5 years. However, it should be pointed out that this estimate is based on a simple static life table. Only through the use of more dynamic models that introduce uncertainty and stochasticity will the full effects of the changes in life history, emigration and immigration, increases or decreases of fishing mortality and recruitment variability on population growth be determined.

Detecting real differences in growth estimates may be difficult (Cailliet *et al.* 1990; Tanaka *et al.* 1990). Differences in vertebral preparation, sample size and in band

counting experience could produce variation in growth rates that are not real. Even though we could not acquire the original vertebral samples, we attempted to minimize some source of bias by re-analyzing the size-at-age data from Branstetter's (1987) study. We do contend that the difference in growth rates could be due, in part, to differences in methodology and sample size, yet it should be noted that both studies counted winter marks from validated growth bands.

It could be argued that growth of this species was not described accurately for the earlier time period because of inadequate sample size for some ages in Branstetter's (1987) study. However, using back-calculated size-at-age to fill in for missing ages (Cailliet 1990) and fitting the von Bertalanffy growth equation to those estimates resulted in similar growth rates and estimates of theoretical maximum size ($K = 0.33$, $L_\infty = 111.1$) to those found using observed size-at-age data. A study on the age and growth of male Atlantic sharpnose sharks collected during 1979–1980 by Parsons (1985) also reported lower growth coefficients ($K = 0.45$) than those determined during 1998–2001. Moreover, mean back-calculated size-at-age was significantly larger ($P < 0.05$) for younger ages (0.0–2.5) collected in 1998–2001 than those from 1984, in spite of the problems associated with using back-calculated size-at-age (Walker *et al.* 1998).

Length-selective fishing mortality caused differences in observed growth rates for gummy shark from two time periods (Moulton *et al.* 1992; Walker *et al.* 1998). This length-selective fishing mortality, or Phenomenon of Apparent Change in Growth Rate, occurs when gill-nets of median selectivity remove from the population large young animals and smaller older animals. The overall effect is that the sampling gear collects more fast-growing sharks, fewer large young sharks and small old sharks. Walker *et al.* (1998) showed that these effects can produce distorted growth curves. By using gill-nets of multiple mesh sizes and the same gear throughout our study, we attempted to minimize any bias associated with the Phenomenon of Apparent Change in Growth Rate. Moreover, a recent study on gill-net selectivity using the same gill-nets as those in the present study found that Atlantic sharpnose sharks have a broad selection curve and all sizes (34–104 cm TL) and ages (0.0–9.5+) of sharks are captured (Carlson and Cortés 2003). A further examination of this effect could be investigated using simulated models, but was out of the scope of the present study.

The increase in observed growth rate for Atlantic sharpnose sharks from 1998–2001 could be attributable to community effects. An alternative hypothesis is that the reduction in large coastal sharks, such as blacktip sharks, in the Gulf of Mexico since the early 1980s has reduced interspecific competition, thus increasing food availability for Atlantic sharpnose sharks. Although no published

quantitative studies of diet or trophic interactions are available for these species, preliminary evidence suggests that juvenile blacktip sharks and adult Atlantic sharpnose sharks share similar food niches (D. Bethea, North Carolina State University, personal communication). Kato (1987) proposed that the increase in growth rate and decrease in maturity found in minke whales *Balaenoptera acutorstrata* were attributable to reduced competition for food with depleted stocks of blue whales *B. musculus* and fin whales *B. physalus*. Further study on the diet and niche relationships of these and other sharks will be necessary to evaluate such hypotheses.

Measuring compensation in populations can be complicated by variation in year-class cohort strength as a result of density independent factors. Sharks are generally regarded to be K-selected species and the relationship between adult stock and recruitment is thought to be close to linear (Holden 1977). We could not rule out that changes measured in the present study were the result of variation in abundance resulting from abiotic factors, such as yearly changes in climate. Unlike r-selected teleosts, measuring the magnitude of any compensation is constrained by the low productivity of many species of sharks. The further lack of a standardized long-term monitoring program to document shark population stability further complicates differentiating between the source and magnitude of the compensatory response.

With the decline in the population of Atlantic sharpnose sharks (Cortes 2002*a*; Simpfendorfer and Burgess 2002), the observed decrease in length and age at maturity and increased growth rate lends support to the hypothesis of a density dependent compensatory response. However, there are many other competing hypotheses, including sampling bias, phenotypic and demographic variation, changes in environmental conditions and temporal and spatial variation among and within stocks, which may account for the observed changes in growth and maturity. To properly address these and other density dependent effects would require complex stochastic demographic and populations models. Although this was not within the goal of the present study, future analysis should investigate these hypotheses.

Acknowledgments

References

Beamish, R. J., and Fournier, D. A. (1981). A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 982–3.

Branstetter, S. (1987). Age and growth validation of newborn sharks held in laboratory aquaria, and comments on the life history of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. *Copeia* **1987**, 291–300.

Cailliet, G. M. (1990). Elasmobranch age determination and verification: an updated review. In 'Elasmobranchs as Living Resources: Advances in Biology, Ecology, Systematics and the Status of the Fisheries'. NOAA Technical Report NMFS 90. (Eds H. L. Pratt Jr, S. H. Gruber and T. Taniuchi.) pp. 157–65. (US Department of Commerce, National Oceanic and Atmospheric Administration: Silver Springs, MD, USA.)

Cailliet, G. M., Yudin, K. G., Tanaka, S., and Taniuchi, T. (1990). Growth characteristics of two populations of *Mustelus manazo* from Japan based on cross-reading vertebral bands. In 'Elasmobranchs as Living Resources: Advances in Biology, Ecology, Systematics and the Status of the Fisheries'. NOAA Technical Report NMFS 90. (Eds H. L. Pratt Jr, S. H. Gruber and T. Taniuchi.) pp. 167–176. (US Department of Commerce, National Oceanic and Atmospheric Administration: Silver Springs, MD, USA.)

Carlson, J. K., and Baremore, I. E. (2002). 'Changes in Biological Parameters of Atlantic Sharpnose Shark, *Rhizoprionodon terraenovae*, in the Gulf of Mexico: Evidence for Density-dependent Regulation?' NAFO SCR Document 02/128. (North Atlantic Fisheries Organization: Dartmouth, Canada.)

Carlson, J. K., and Cortés, E. (2003). Gillnet selectivity of small coastal sharks off the southeastern United States. *Fisheries Research* **60**, 405–14.

Carlson, J. K., Cortés, E., and Bethea, D. M. (2003). Life history and population dynamics of the finetooth shark, *Carcharhinus isodon*, in the northeastern Gulf of Mexico. *Fishery Bulletin U. S.* **101**, 281–92.

Cortés, E. (1995). Demographic analysis of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, in the Gulf of Mexico. *Fishery Bulletin U. S.* **93**, 57–66.

Cortés, E. (1998). Demographic analysis as an aid in shark stock assessment and management. *Fisheries Research* **39**, 199–208.

Cortés, E. (2002*a*). 'Stock Assessment of Small Coastal Sharks in the US Atlantic and Gulf of Mexico.' Sustainable Fisheries Division Contribution SFD-01/02-152. (NOAA/National Marine Fisheries Service, Southeast Fisheries Science Center: Panama City.)

Cortés, E. (2002*b*). Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. *Conservation Biology* **16**, 1–15.

Cortés, E., and Gruber, S. H. (1994). Effect of ration size on growth and gross conversion efficiency of young lemon sharks, *Negaprion brevirostris*. *Journal of Fish Biology* **44**, 331–41.

Fabens, A. J. (1965). Properties and fitting of the von Bertalanffy growth curve. *Growth* **29**, 265–89.

Frisk, M. G., Miller, T. J., and Fogarty, M. J. (2002). The population dynamics of little skate *Leucoraja erinacea*, winter skate *Leucoraja ocellata*, and barndoor skate *Dipturus laevis*: predicting exploitation limits using matrix analyses. *ICES Journal of Marine Science* **59**, 576–86.

Holden, M. J. (1973). Are long-term sustainable fisheries for elasmobranchs possible? *Rappports et Procès-Verbaux des Réunions Conseil International Pour l'Exploration de la Mer* **64**, 360–7.

Holden, M. J. (1977). Elasmobranchs. In 'Fish population dynamics'. (Ed. J. A. Gulland.) pp. 187–215. (John Wiley & Sons: London.)

Kato, H. (1987). Density dependent changes in growth parameters of the southern minke whale. *Scientific Report of Whales Research Institut*e **38**, 48–73.

Kohler, N. E., Casey, J. G., and Turner, P. A. (1998). NMFS cooperative shark tagging program, 1962–93: an atlas of shark tag and recapture information. *Marine Fisheries Review* **60**, 1–87

Kimura, D. K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin U. S.* **77**, 765–76.

Mollet, H. F., Cliff, G., Pratt, H. L., and Stevens, J. D. (2000). Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. *Fishery Bulletin U. S.* **98**, 299–318.

Moulton, P. L., Walker, T. I., and Saddlier, S. R. (1992). Age and growth studies of gummy shark, *Mustelus antarcticus* Günther, and school shark, *Galeorhinus galeus* (Linnaeus), from southern Australian waters. *Australian Journal of Marine and Freshwater Research* **43**, 1241–67.

National Marine Fisheries Service (1993). 'Fishery Management Plan for Sharks of the Atlantic Ocean.' (U. S. Department of Commerce, National Oceanic and Atmospheric Administration: Silver Springs.)

Parsons, G. R. (1983). The reproductive biology of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae* (Richardson). *Fishery Bulletin U. S.* **81**, 61–73.

Parsons, G. R. (1985). Growth and age estimates of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*: a comparison of techniques. *Copeia* **1985**, 80–5.

Rose, K. A., Cowan, J. H., Winemiller, K. O., Meyers, R. A., and Hilborn, R. (2001). Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries* **2**, 293–327.

Simpfendorfer, C. A., and Burgess, G. A. (2002). 'Assessment of the Status of the Atlantic Sharpnose Shark (*Rhizoprionodon terraenovae*) using an Age-structured Population Model.' NAFO SCR Doc. 02/116. (North Atlantic Fisheries Organization: Dartmouth, Canada.)

Sminkey, T. R., and Musick, J. A. (1995). Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. *Copeia* **1995**, 871–83.

Smith, S. E., Au, D. W., and Show, C. (1998). Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research* **49**, 663–78.

Tanaka, S., Cailliet, G. M., and Yudin, K. G. (1990). Differences in growth of the blue shark, *Prionace glauca*: technique or population. In 'Elasmobranchs as Living Resources: Advances in Biology, Ecology, Systematics and the Status of the Fisheries'. NOAA Technical Report NMFS 90. (Eds H. L. Pratt Jr, S. H. Gruber and T. Taniuchi.) pp. 177–187. (US Department of Commerce, National Oceanic and Atmospheric Administration: Silver Springs, MD, USA.)

Taylor, L., and Wisner, M. (1988). Growth rates of captive blacktip reef sharks (*Carcharhinus melanopterus*). *Bulletin de l'Institut Océanographique, Monaco* **5**, 211–17.

von Bertalanffy, L. (1938). A quantitative theory of organic growth (inquiries on growth laws. II). *Human Biology* **10**, 181–213.

Walker, T. I. (1992). A fishery simulation model for sharks applied to the gummy shark, *Mustelus antarcticus* Günther, from southern Australian waters. *Australian Journal of Marine and Freshwater Research* **43**, 195–212.

Walker, T. I., Taylor, B. L., Hudson, R. J., and Cottier, J. P. (1998). The phenomenon of apparent change of growth rate in gummy shark (*Mustelus antarcticus*) harvested off southern Australia. *Fisheries Research* **39**, 139–63.

Wood, C. C., Ketchen, K. S., and Beamish, R. J. (1979). Population dynamics of spiny dogfish (*Squalus acanthias*) in British Columbia waters. *Journal of the Fisheries Research Board Canada* **36**, 647–56.

Zar, J. H. (1984). 'Biostatistical Analysis.' (Prentice Hall: Englewood Cliff.)